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Research Article

Fossil Trichoptera embedded in mid-Cretaceous Burmese amber*

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Abstract

The paper gives an overview of Trichoptera found as adults in mid-Cretaceous Burmese amber from about 100 million years ago. Fifty-eight extinct species are listed, three of which are still described here: *Paduniella cretacea* **sp. nov.**, *Palerasnitsynus vilarinoi* **sp. nov.**, *Palleptocerus kuranishii* **sp. nov.** The extinct subfamily Palerasnitsyninae **stat. nov.** of the family Xiphocentronidae is established and the extinct *Bipectinata orientalis* **comb. nov.** is transferred from the family Calamoceratidae to the family Odontoceridae. The extinct family Lepidochlamidae Wang et al., 2022, **stat. nov.** is transferred to the superfamily Leptoceroidea.

The fifty-eight caddisflies of Burmese amber are distributed among twenty-one genera and fourteen families, of which fifteen genera and four families are also extinct. The large time distance between extinct and extant organisms makes the assignment to the extant genera and families difficult, because the higher taxa are defined according to the species living today and often do not or hardly correspond to the earlier species and their adaptations. Furthermore, in line with the hypothesis of a Gondwanan origin of Burmese amber, some embedded Trichopterans are discussed as relict descendants of Gondwanan Trichoptera, e.g. the family Palleptoceridae and the Xiphocentronid subfamily Palerasnitsyninae.

Key Words

Evolutionary history, Fossil record, Gondwana, Trichoptera checklist, West Burma Block

Introduction

TDA Cockerell described a fossil species embedded in Burmese amber, *Plecophlebus nebulosus* Cockerell (1917), and assigned it to the order Trichoptera. A later examination of the holotype by Botosaneanu (1981) showed that this species does not belong to the order Trichoptera, but to Homoptera (Auchenorrhyncha). However, at the same time Botosaneanu described another finding in Burmese amber that clearly belonged to the order Trichoptera: *Burminoptila bemeneha* Botosaneanu (1981) (Hydroptilidae). It took 24 years for a second description of a caddisfly, *Wormaldia myanmari* Wichard & Poinar, 2005 (Philopotamidae). This marked the beginning of the continuous study of the Trichoptera in mid-Cretaceous Burmese amber. To date, 58 species of caddisflies have been described, distributed among 21 genera and 14 families.

In this paper, all described species are presented in an updated checklist, including the institutional repositories of all their deposited holotypes. In addition to this overview, special attention is given to the superfamilies Psychomyioidea and Leptoceroidea, which include remarkable extinct species embedded in mid-Cretaceous Burmese amber.

Materials and methods

The amber material was collected by local people in the Hukawng Valley of northern Myanmar, (Myitkyina District, Kachin State) (Fig. 1) and derives from an amber bearing layer, which is not exposed to surface but is extending at a depth of 2–15 m (Cruickshank and Ko 2003). The amber dates from the middle Cretaceous (Cenomanian) period about 98.8 ± 0.6 Ma ago (Shi et al. 2012).

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Figure 1. Camp and preparations for Burmese amber digging in the Hukawng Valley (from Bo Wang).

The Burmese amber with the embedded Trichopteran inclusions was cut, facegrinded and polished using a cutting machine and a polishing machine, a RotoPol-25 (Struers), with grinding paper for metallography: 800, 1200, 2500, and 4000 grit. Colour photographs were produced for the documentation of specimens. A Leica M420 macroscope with Apozoom 1:6 was used in combination with Canon EOS 80D and Canon EOS R, EOS 3.0 utility software and Zerene Stacker software. Measurements made with a Leica SApo ocular micrometer.

Depositories

All listed and described holotype specimens of Trichoptera in mid-Cretaceous Burmese amber are kept and preserved in the following institutional repositories:

NIGP	Nanjing Institute of Geology and Palaeontology, Nanjing, China
CNUB	Capital Normal University, Beijing, China
RPX	Ruipoxuan Amber Museum Jinan, China
ZFMK	Zoological Research Museum Alexander Koenig, Bonn, Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
ZSM	Zoologische Staatssammlung München, Germany
MP.I	Museum für Naturkunde Berlin, Germany
B.M.(N.H.)	British Museum (Natural History), London, GB
Coll POINAR	Oregon State University, Corvallis, USA

Abbreviations

Wing venation:

I, II, III, IV, V	=	apical forks I, II, III, IV, V.
TC	=	thyridial cell.

Male genitalia:

inf app	=	inferior appendage.
pre app	=	preanal appendage (cercus).
phal	=	phallic apparatus
harp	=	harpago (apical segment of an inferior appendage).
coxo	=	coxopodite (basal segment of an inferior appendage).
int pro	=	intermediate process.
med pro	=	medio-distad process.
IX	=	abdominal segment IX.

Checklist of the Trichoptera in mid-Cretaceous Burmese amber

The following current checklist (Table 1) includes 58 extinct species, distributed among 21 genera and 14 families. Of the 14 families, 6 families belong to the suborder Annulipalpia, the 8 other family to the suborder Integripalpia, of which 4 families are extinct and only found in Burmese Amber. Of the 21 listed genera, the majority of 15 genera is extinct and only 6 genera are extant.

Table 1. Fossil Trichoptera embedded in mid-Cretaceous Burmese amber. Species checklist with evidence of deposited holotypes.

Suborder Annulipalpia Martynov, 1924:		
Family Polycentropodidae Ulmer, 1903		
Electrocentropus dilucidus Wichard, 2021	ZFMK	TRI000817
Neucentropus macularis (Wang et al., 2019)	CNUB	TRI-MA-2016505
Neureclipsis triangular Wichard & Xu, 2022	NIGP	200021
Neurecipsis burmanica Wichard & Wang, 2016	SMNS	2305 22015
Neureclipsis acuta Wichard & Xu, 2022	NIGP	200022
Neureclipsis obtuse Wichard & Xu, 2022	NIGP	200023
Plectrocnemia ohlhoffi Wichard & Xu, 2022	ZFMK	TRI000834
Plectrocnemia bowangi Wichard & Xu, 2022	NIGP	200024
Family Kambaitipsychidae Malicky, 1991		
Myanpsyche malaisei (Wichard & Wang, 2019)	NIGP	170801
Family Pseudoneureclipsidae Ulmer, 1951		
Amberclipsis elegans Wichard, Müller & Fischer, 2022	ZSM	TRI-AMB001
Amberclipsis oblongus Wichard, Müller & Fischer, 2022	ZFMK	TRI000823

Amberclipsis simplex Wichard, Müller & Fischer, 2022	ZFMK	TRI000824
Protoclipsis picteti Wichard, Müller & Fischer, 2022	ZFMK	TRI000826
Protoclipsis roeseli Wichard, Müller & Fischer, 2022	ZFMK	TRI000827
Protoclipsis ulmeri Wichard, Müller & Fischer, 2022	ZFMK	TRI000825
Family Psychomyiidae Walker, 1852		
Paduniella cretacea **sp. nov.**	ZFMK	TRI000835
Family Xiphocentronidae Ross, 1949		
Subfamily †Palerasnitsyninae stat. nov.		
Palerasnitsynus ohlhoffi Wichard, Ross & Ross, 2011	NIGP	157001
Palerasnitsynus furcatis Wichard, Müller & Wang, 2018	MB.I	7304
Palerasnitsynus gracilis Wichard, Müller & Wang, 2018	NIGP	154981
Palerasnitsynus lepidus Wichard, Müller & Wang, 2018	MB.I	7300
Palerasnitsynus spinosus Wichard, Müller & Wang, 2018	MB.I	7299
Palerasnitsynus subglobolus Wichard, Müller & Wang, 2018	NIGP	154986
Palerasnitsynus subgrandis Wichard, Müller & Wang, 2018	NIGP	154982
Palerasnitsynus sukatchevae Wichard, Müller & Wang, 2018	MB.I	7298
Palerasnitsynus vulgaris Wichard, Müller & Wang, 2018	MB.I	7301
Palerasnitsynus vilarinoi **sp. nov.**	ZFMK	TRI000836
Family Philopotamidae Stephens, 1829		
Wormaldia cercifurcata Wichard, Müller & Wang, 2020	NIGP	172212
Wormaldia cercilonga Wichard, Müller & Wang, 2020	NIGP	172211
Wormaldia cretacea Wichard & Wang, 2016	NIGP	156999
Wormaldia myanmari Wichard & Poinar, 2005	Coll POINAR	
Wormaldia resina Wichard & Wang, 2016	NIGP	157000
Wormaldia squamosa Wichard, Müller & Wang, 2020	ZFMK	TRI000821
Wormaldia transversa Wichard, Müller & Wang, 2020	ZFMK	TRI000820
Wormaldia diplobifurca Wang, Zhang, Shi & Ren, 2021	CNUB	TRI-MA-2016506
Wormaldia denticulata Wang, Zhang, Shi & Ren, 2021	CNUB	TRI-MA-2016507
Suborder Integripalpia Martinov, 1924:		
Family Hydroptilidae Stephens, 1836		
Subfamily †Burminoptilinae Wichard, 2021		
Burminoptila bemeneha Botosaneanu, 1981	B.M.(N.H.)	20180
Cretacoptila botosaneanui Wichard, 2021	NIGP	163573
Infraorder Brevitentoria Weaver, 1984:		
Family Helicopsychidae Ulmer, (1906) 1912		
Cretahelicopsyche liuyani Wichard, Espeland, & Wang, 2018	RPX	18001
Family †Burmapsychidae Wichard, 2021		
Burmapsyche comosa Wichard, Neumann, Müller, & Wang, 2018	NIGP	166872
Burmapsyche palpifurcata Wichard, Neumann, Müller, & Wang, 2018	NIGP	166873
Burmapsyche wolframmeyi Wichard & Kuranishi, 2023	SEHU	54024
Family †Cretapsychidae Wichard, 2021		
Cretapsyche circula Wichard, Neumann, Müller & Wang, 2018	MB.I.	7271
Cretapsyche elegans Wichard, Neumann, Müller & Wang, 2018	MB.I.	7273
Cretapsyche insueta Wichard, Neumann, Müller & Wang, 2018	MB.I.	7272
Cretapsyche palpinova Wichard & Neumann, 2019	MB.I.	7340
Cretapsyche kachini Wichard & Espeland, 2022	ZFMK	TRI000829
Cretapsyche myanmari Wichard & Espeland, 2022	ZFMK	TRI000830
Family Calamoceratidae Ulmer, 1916		
Cretaganonema dongi Wichard, Espeland & Wang, 2018	NIGP	154571
Family Odontoceridae Wallengren, 1891		
Bipectinata orientalis Wichard, Espeland, Müller & Wang, 2020, **comb. nov.**	NIGP	172206
Palaeopsilotreta xiai Wichard & Wang, 2017	NIGP	164781
Palaeopsilotreta burmanica Wichard, Espeland, Müller & Wang, 2020	ZFMK	TRI000813
Palaeopsilotreta cretacea Wichard, Espeland, Müller & Wang, 2020	ZFMK	TRI000814
Palaeopsilotreta succini Wichard, Müller & Xu, 2021	ZFMK	TRI000822
Palaeopsilotreta kachini Wichard, Müller & Xu, 2021	NIGP	175454
Psilotreta fossilis Wichard, Müller & Xu, 2021	NIGP	175453
Family †Lepidochlamidae Wang et al., 2022, **stat. nov.**		
Lepidochlamus nodosa Wang et al., 2022	CNUB	TRI-MA-2015501
Family †Palleptoceridae Wichard & Müller, 2022		
Palleptocerus grimaldii Wichard & Müller, 2022	ZFMK	TRI000831
Palleptocerus kuranishii **sp. nov.**	SEHU	45040

Systematic palaeontology

Order Trichoptera Kirby, 1813
Suborder Annulipalpia Martynov, 1924
Superfamily Psychomyioidea Walker, 1852
Family Psychomyiidae Walker, 1852
Genus *Paduniella* Ulmer, 1913

***Paduniella cretacea* sp. nov.**

https://zoobank.org/8CE659BD-2BCD-4080-ABDC-41B6DF7DCB17

Fig. 2

Holotype. Male-specimen deposited Zoological Research Museum Alexander Koenig, Bonn, Germany, Inventory no.: ZFMK-TRI000835 (ex coll. Patrick Müller)

Preservation. The fossil male is well preserved in amber. Antennae present, as well as the six-segmented maxillary palps. The labial palps are not recognizable. The forewings show the venation well, the hind wings are unfortunately hidden. The inferior appendages of the male genital are visible from ventral.

Etymology. The extinct *Paduniella* species is named after its geological age of the Cretaceous period (latin: Cretaceum).

Description. Male, forewings ca. 2.8 mm long, antennae about half as long as forewing. Maxillary palps each six-segmented (Fig. 2C); labial palps not visible. Each forewing has forks II, III, IV, and V; hindwings not visible. In ventral view (Fig. 2B), male genitalia have deep, bifurcated inferior processes each with an elongate, overhanging process that is tapered and slightly curved apically. In lateral view (Fig. 2D), a slender median process is visible.

Diagnosis. The male genitalia of *Paduniella* species have inferior appendages whose apices are either bifurcated or unbifurcated (Li and Morse 1997). The extinct *Paduniella cretacea* sp. nov. has similar to the extant species, *P. tanidai* from Japan (Nishimoto, 2011) and *P. burmana* (Johanson & Olah, 2010) from the Oriental region, bifurcated inferior appendages that are deeply incised at the apex rather than superficially notched. The fossil species is distinguished from the two extant species in the deeply bifurcated apex of the inferior appendage because one fork is needle-like, acuminate, and curved and clearly protrudes above the other stouter fork. *Paduniella cretacea* **sp. nov.** is the first fossil *Paduniella* species found in ca. 100 million year old mid-Cretaceous Burmese amber.

Family Xiphocentronidae Ross, 1949

Subfamily †Palerasnitsyninae stat. nov.

Type genus. *Palerasnitsynus* Wichard, Ross & Ross, 2011.

Subfamily diagnosis. The species of the extinct subfamily Palerasnitsyninae are characterised by the combination of the fore and hind wings' characters: in forewings by the presence of forks II, IV, V and by the absence of forks I and III and in hind wings by the presence of forks II and V and by the absence of the forks I, III, IV (Fig. 3B). Furthermore, the adults possess latero-apical dark sporns at the 3rd maxillary palp segments (Fig. 3A).

Systematic position. The extinct genus *Palerasnitsynus*, with currently 10 species, was found in the Oriental mid-Cretaceous Burmese amber and initially placed in the family Psychomyiidae (Wichard et al. 2011). The wing venation is remarkably reduced, with only apical forks II, IV, V in forewings and apical forks II and V in hind wings. The reduction of forewing venations with the absence of forks I and III and of hind wing venations with the absence of forks I, III and IV is observed in some Xiphocentronids, but not in the family Psychomyiidae. This combination of reduced forewings and hindwings is significantly true for the family Xiphocentronidae. Based on these characters, it is proposed to transfer the genus *Palerasnitsynus* to family Xiphocentronidae and to establish an extinct subfamily Palerasnitsyninae stat. nov. Its species are the oldest Xiphocentronids with a geological age of about 100 million years.

In Burmese amber, the species of the subfamily Palerasnitsyninae are certainly among the smallest caddisflies, reaching forewing lengths of only 1.8–2.6 mm (Wichard et al. 2011, 2018b). With an abundance of almost 40% of caddisflies, *Palerasnitsynus* species dominate the picture of caddisflies in the Burmese amber. They obviously have a tendency to swarm, as up to 100 embedded individuals have been counted in some ambers (Fig. 3C).

Genus *Palerasnitsynus* Wichard, Ross & Ross, 2011

Type species. *Palerasnitsynus ohlhoffi* Wichard, Ross & Ross, 2011.

Genus diagnosis. The extinct genus *Palerasnitsynus* is characterised by the combination of the fore and hind wings' characters: in forewings by the presence of forks II, IV, V and by the absence of forks I and III and in hind wings by the presence of forks II and V and by the absence of the forks I, III, IV (Fig. 3B). Furthermore the adults possess latero-apical dark sporns at the 3rd maxillary palp segments (Fig. 3A).

***Palerasnitsynus vilarinoi* sp. nov.**

https://zoobank.org/53E80DF4-3FAB-4AEA-9418-B5796D02F00D

Fig. 4

Types. A small Burmese amber contains three males, which are the holotype and two paratypes attesting to the new species. The amber is deposited Zoological Research Museum Alexander Koenig, Bonn, Germany, inventory no.: ZFMK-TRI000836 (BUB 3585 ex coll. Patrick Müller).

Preservation. Two males, preserved in varying condition, are embedded in a single amber (Fig. 4A). The

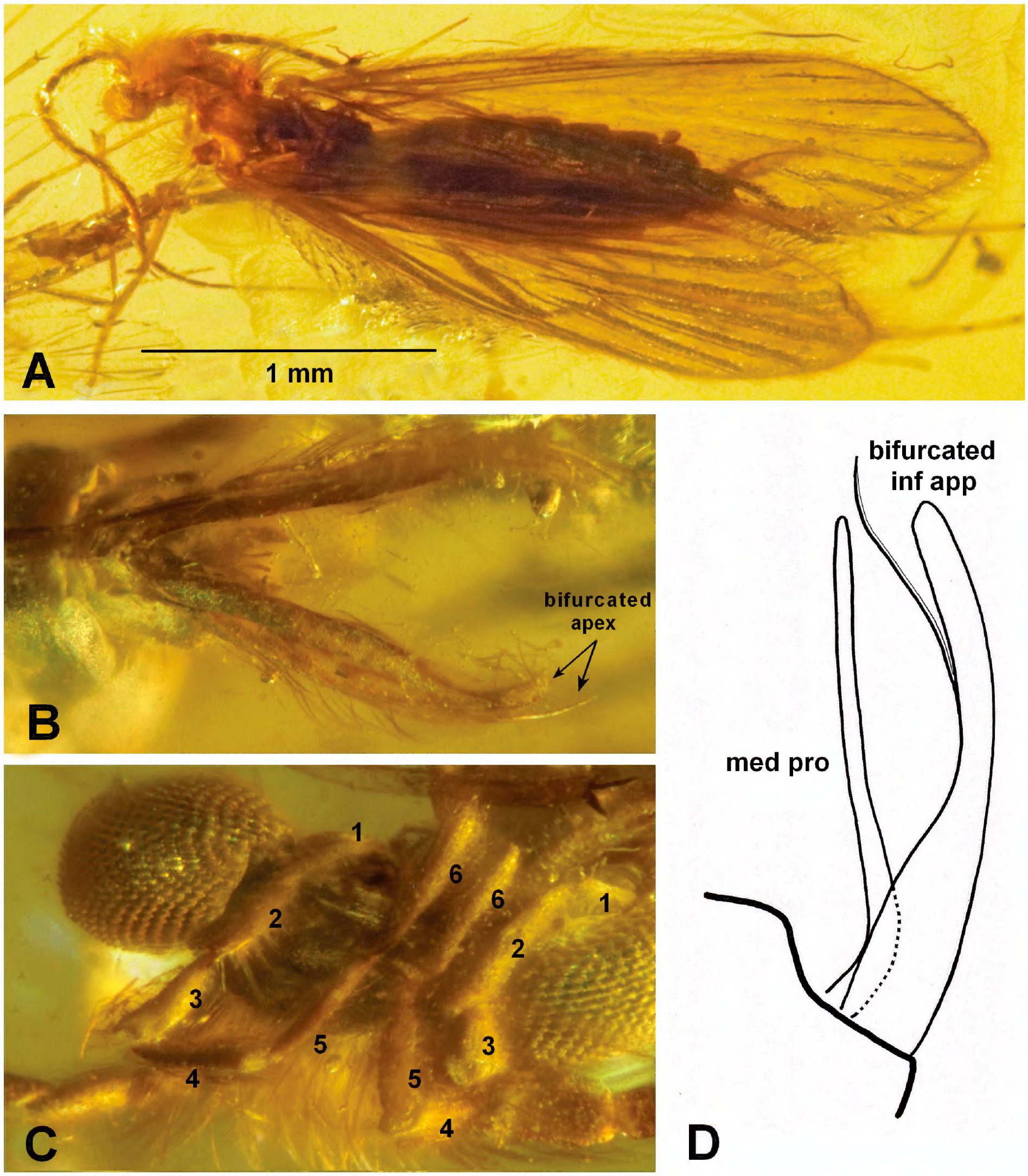

Figure 2. *Paduniella cretacea* sp. nov. in mid-Cretaceous Burmese amber, male holotype (Inventory no.: ZFMK-TRI0008359. **A.** Male in ventral view; **B.** Paired bifurcated inferior appendages in ventral view; **C.** Paired 6-segmented maxillary palps; **D.** Drawing of bifurcated inferior appendages (inf app) and median process (med pro) in lateral view.

holotype is completely preserved, from dorsal and ventral view. From ventral the pair of the genital inferior appendages is clearly visible. The paratype shows the genital laterally, although not absolutely clear. Forewings and hind wings are spread apart in the paratype.

Etymology. The new species is dedicated to Albane Vilarino, Brasil, who pointed out that the extinct genus *Palerasnitsynus* may belong to the family Xiphocentronidae.

Description. Male, adult with general characters of the genus, forewing length ca. 2 mm, antennae with about 20 cylindrical flagellomeres, plus scapus and pedicellus.

***Genitalia*:** In ventral view (Fig. 4B), the inferior appendages are almost parallel, the separation of the basal coxopodite and the attached harpago is only weakly indicated, possibly they are fused. The inside flanks of the inferior appendage are loosely equipped with long and strong setae. The basal coxopodite is somewhat elongated and

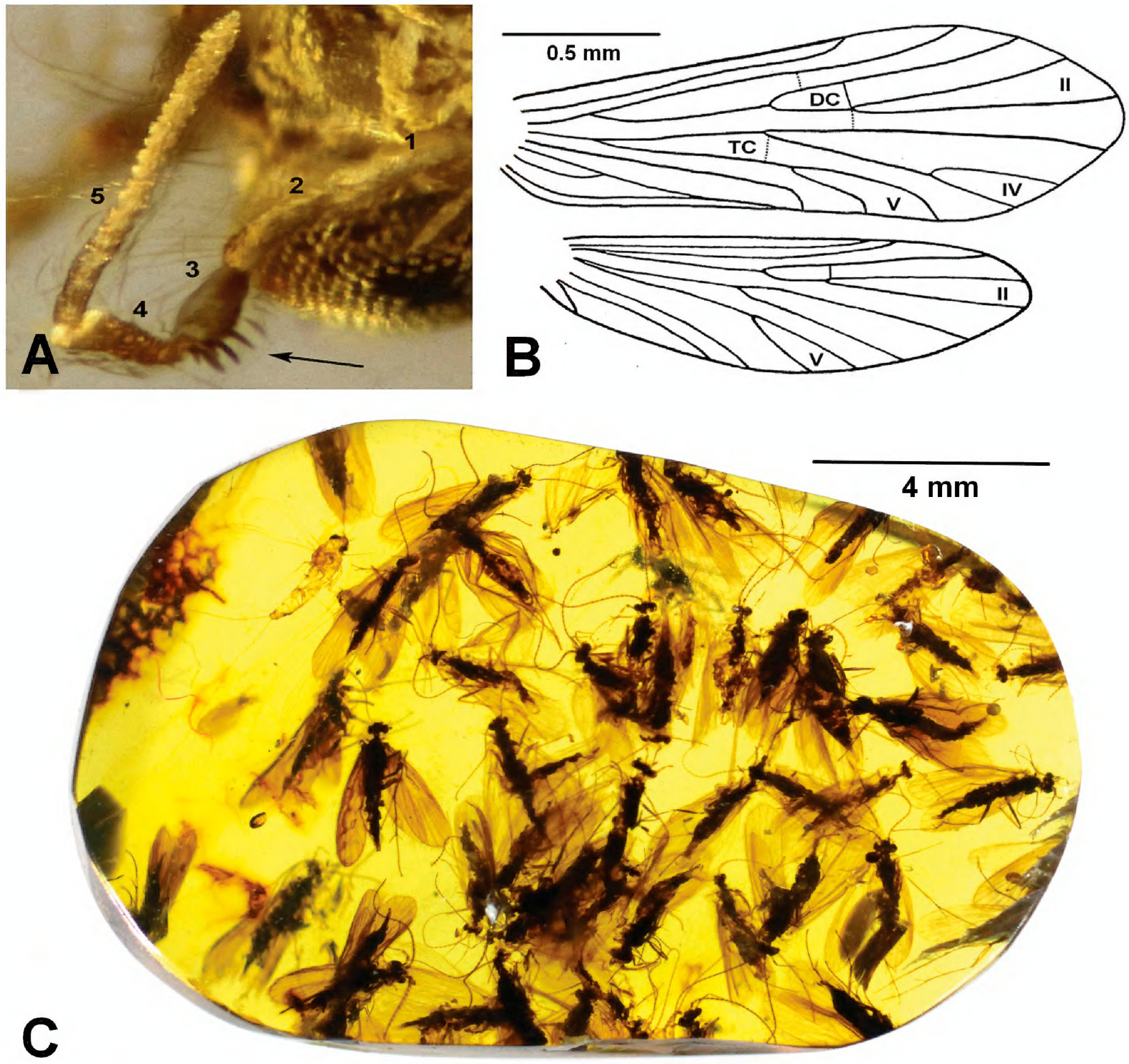

Figure 3. Genus *Palerasnitsynus* in mid–Cretaceous Burmese amber. **A.** Typical dark sporns at the 3rd maxillary palp segment; **B.** Typical presence of forks II, IV, V in forewings and of forks II and V in hind wings; **C.** *Palerasnitsynus* swarming activities.

baso-laterally rounded, the harpago probably only slightly longer than the coxopodite. The apex of each harpago bears a dark spiny head with densified spines of nearly equal length. The needled heads of the adjacent harpagoes face each other (Fig. 4B). In lateral view (Fig. 4C), the male genital shows a pair of parallel intermediate processes (int pro) which in length barely reach the level of the medio-lateral process (med pro) which originated from the coxopodite is elongate-round and bears a bush of long setae. The intermediate process is needle-shaped, somewhat broadened in the middle, and tapers toward the apex to a ventrally inclined dark tip. The pair of short preanal appendages and a short needle-like process with dark tip, dorsally inclined, are not clearly visible.

Diagnosis.: *Palerasnitsynus vilarinoi* sp. nov. is exclusively characterized by the latero-apical dark sporns at the 3rd maxillary palp segments and by the presence of forks II, IV, V in forewings and by the presence of forks II and V in hind wings. The new species is distinguished from all other species of *Palerasnitsynus* by the typical dark spiny head of each harpago apex facing each other with their spiny heads (Fig. 4B). The elongate needle-like intermediate processes terminate in a ventrally inclined tip. However, they do not extend longitudinally beyond the medio-lateral process of the coxopodite (Fig. 4C).

Suborder Integripalpia Martynov, 1924
Superfamily Leptoceroidea Leach, 1815
Family Odontoceridae Wallengren, 1891

Bipectinata orientalis Wichard et al., 2020b, comb. nov.

Fig. 5

Systematic position. *Bipectinata orientalis* was not originally placed in the family Odontoceridae, but was

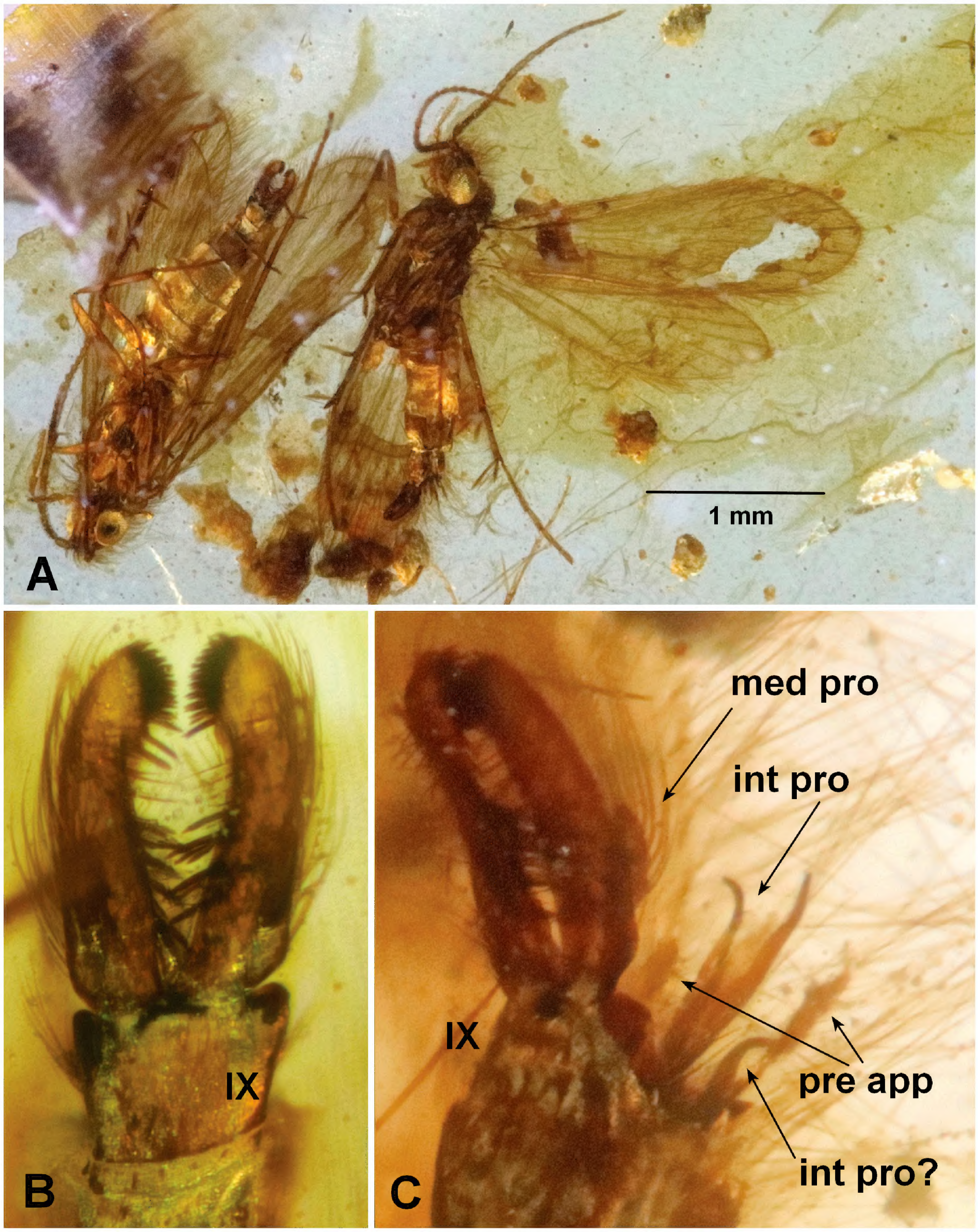

Figure 4. *Palerasnitsynus vilarinoi* sp. nov. in mid–Cretaceous Burmese amber (inventory no.: ZFMK-TRI000836). **A.** Holotype (left) and paratype (right); **B.** Holotype inferior appendages in ventral view; **C.** Paratype male genitalia in lateral view.

initially assigned to Calamoceratidae (Wichard et al. 2020), because the presence of wing fork IV on the forewing is not common to extant Odontoceridae. Nevertheless, characteristic features of the family Odontoceridae are synapomorphically present in the genus *Bipectinata*, such as five-segmented maxillary palps with a terminal segment not flexible or annulated, lack of ocelli, tibial spur formula 2/4/4; in forewings fork I present, discoidal cell closed and median cell absent. In addition, genus *Bipectinata* is closely related to the odontocerid genus

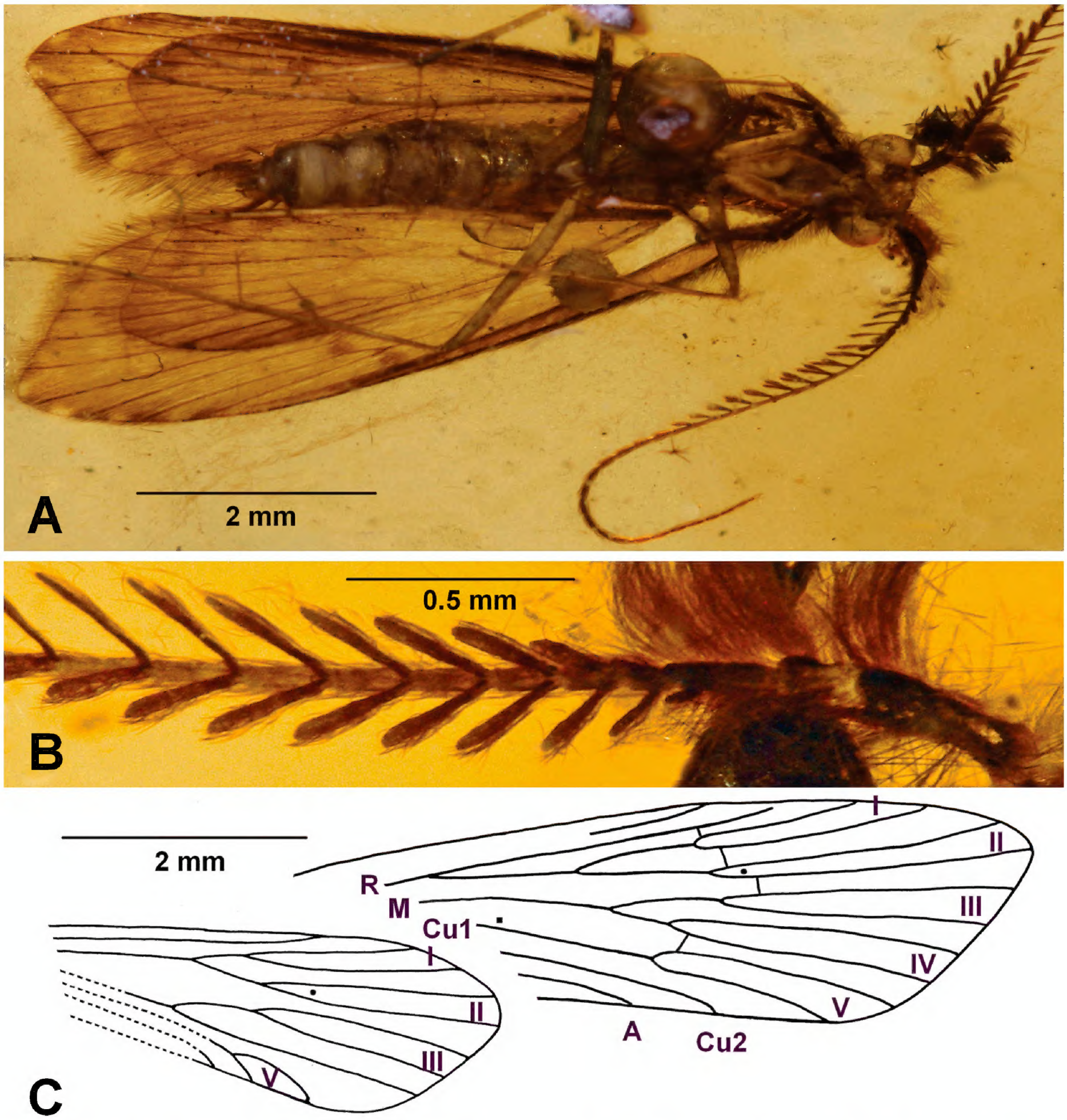

Figure 5. *Bipectinata orientalis* Wichard et al., 2020b. **A.** Male in ventral view; **B.** Bipectinate antenna; **C.** Plesiomorphic forewing venation with five apical forks.

Palaeopsilotreta, whose common synapomorphies involve a variable forewing media and the bipectinate antennae (Fig. 5B).

In trichopteran adults a complete set of five apical forks on the forewings is clearly a plesiomorphic character (Comstock 1918; Holzenthal et al. 2007). A reduction of the original wing venation and the reduction of apical forks are derived in many adults, especially within the superfamily Leptoceroidea. However, the extinct *Bipectinata orientalis* from the middle Cretaceous is characterized by the original arrangement of five apical forks in the forewing venation (Fig. 5C). This feature distinguishes it from the closely related species of the genus *Palaeopsilotreta*.

Family †Lepidochlamidae Wang et al., 2022, stat. nov.

Type genus + species. *Lepidochlamus nodosa* Wang et al., 2022.

Family diagnosis (based on Wang et al. 2022). Ocelli absent; antenna longer than forewing, at least 71 flagellomeres preserved; maxillary palpus five-segmented, terminal palpomere V longest, not annulated, shorter than combined lengths of preceding four palpomeres. Male forewing with forks I, III, and V; all crossveins absent. Hind wing covered with a single layer of angustifoliate scales; wing venation unknown. Tibial spur formula 2/4/4.

Systematic position. The monobasic family Lepidochlamidae Wang et al., 2022 is transferred to the

Integripalpian infraorder Breviteniotoria and to its superfamily Leptoceroidea: *Lepidochlamus nodosa* is characterized by the absence of ocelli and by the presence of the five-segmented maxillary palps with terminal segment not annulated, the antennae longer than forewings and the mid-tibia with preapical and apical pairs of spurs. The combination of these morphological features clearly points to the superfamily Leptoceroidea (Ross 1967; Weaver 1983, 1984; Frania and Wiggins 1997; Morse 1997).

According to Wang et al. (2022), the "*Lepidochlamidae, whose hindwings are covered with scales, are the sister group of all other caddisflies (Eutrichoptera)*." But as a member of the monobasic family Lepidochlamidae of the superfamily Leptoceroidea it cannot be the oldest representative of the order Trichoptera, forming a sister group relationship to all other Trichoptera, as suggested.

The establishment of the new taxa by Wang et al. (2022) is an overestimation of the scales on its hind wings. Scales on the hind wings of Breviteniorian species do not enforce the exceptional position of the "*early caddisfly evolution*" The scales on the hind wings are not a unique feature. Single-layered scales also cover other hindwings, e.g. *Helicopsyche kariona* Ross, 1975, *Helicopsyche boularia* Ross, 1975 (see Johanson 1998) and both wings together e.g. *Helicopsyche megalochari* Malicky, 1974 as well as forewings, e.g. *Lepidostoma americanum* Flint and Wiggins,1961, *Oecetis pechana* Mosely & Kimmins, 1953. In xiphocentronid genera *Drepanocentron* and *Abaria* scales are found on fore- and hindwings as well on hindwings only (Schmid 1982). Scales on the wings (also called scale-like setae or scaloid setae) are well known in Trichoptera families and are probably derived from primitive setae.

In addition, the wing vein reduction in general and here the forewing venation reduction of *Lepidochlamus nodosa* is clearly phylogenetically derived. The plesiomorphic complete set of five apical forks is reduced by the loss of forks II and IV, which is common in some families of Breviteniotoria as well as in its family Lepidochlamidae. Moreover, the nygmata in fork II and occasionally in the thyridial cell may be absent, and also the crossveins that would occlude the discoidal, medial, and thyridial cells, are not discernable most likely due to the embedding condition in amber. In my experience, the crossveins and nygmata are very difficult or impossible to recognize in amber. Only a comparison of several specimens of the same species allows a reliable statement about the presence or absence of the nygmata and the cross veins. The fossil *Lepidochlamus nodosa* is based on a single specimen, moderately preserved in mid-Cretaceous Burmese amber, kept as holotype no. CNU-TRI-MA-2015501, in Capital Normal University, Beijing, China.

Family †Palleptoceridae Wichard & Müller, 2022

Type genus and species. *Palleptocerus grimaldii* Wichard & Müller, 2022.

Family diagnosis (based on Wichard and Müller 2022). Tibial spur formula 2/4/4. Antennae longer than forewings, flagellomeres cylindrical, elongate. Maxillary palps are five-segmented, terminal segment not annulated. Male forewing fork I and V present, discoidal cell absent. Hind wing exclusively fork V present.

Palleptocerus kuranishii sp. nov.

https://zoobank.org/52C081CE-D53F-410A-81C6-C88806ED9838

Fig. 6

Holotype. Mail-specimen deposited in the Systematic Entomology Collection of Hokkaido University Museum, Japan, inventory number: SEHU-54040 (ex coll. Ryoichi B. Kuranishi: Burmite 2).

Preservation. The fossil is embedded in an oval and polished piece of amber. The adult insect is completely preserved and clearly visible in dorso-ventral aspect. The wings are folded over the body like a saddle roof, making it difficult to see the hind wings. Head is visible, long antennae incomplete in length. Legs also present. In male genitalia, only the anterior paired inferior appendages are often clearly visible ventrally, further genital structures implied visible.

Etymology. The new species is dedicated in honor of the Japanese entomologist and scientist Ryoichi B. Kuranishi. I got to know and appreciate Ryoichi on the occasion of the 17th International Symposium on Trichoptera in Lunz, Austria, September 2022.

Description. ***Head*:** Laterally protruded compound eyes. Ocelli not present. Filiform antennae longer than forewings – incomplete in length, probably 30–40 flagellomeres; scapus conically thickened, pedipalpus small and globular; flagellomeres cylindrical, elongate (Fig. 6B). Five-segmented maxillary palps present, 5th segment not annulated. Labial palps three-segmented, terminal segment longest.

***Wings* (Fig. 6C):** The forewings about 6 mm long. Venation Sc and R1 straight running parallel to the wing margin. R2 + R3 forming fork I present and R4+5 simple, discoidal cells absent. Media two-branched in M1+2 and M3+4. Cu1 two-branched in Cu1a and Cu1b, forming fork V. Crossvein m-cu closing the long thyridial cell. Venation Cu2 running into A at crossvein between Cu1b and Cu2, then A with Cu2 reaching wing margin.

***Tibial spurs*:** 2/4/4.

***Genitalia* (Fig. 6D, E):** In ventral view, the male genitalia equipped with a pair of inferior appendages, each consisting of a dark coxopodite, narrow at the base, distad slightly broadened, overall slightly conical bent, and attached an apically attached harpago slender than the coxopodite, tapers and curves slightly toward the genital middle.

Diagnosis. Ocelli absent. Antennae longer than forewings, flagellomeres elongate. Maxillary palps five-segmented, terminal segment not annulated. Forewings light brown, slightly narrow and apically rounded. In male forewing venation with forks I and V present, discoidal cells open and thyridial cells closed, long. Tibial spurs: 2/4/4. *Palleptocerus kuranishii* sp. nov. is distinguished

Figure 6. *Palleptocerus kuranishii* sp. nov. in mid–Cretaceous Burmese amber, male holotype (inventory number: SEHU-54040). **A.** Male in lateral view; **B.** Excerpt of the antenna with cylindrical, elongate flagellomeres; **C.** Drawing of the forewing venation; **D, E.** Male genitalia with paired inferior appendages in ventral view.

from *P. grimaldii* by a slender body shape and size of 6 mm forewing length and by the form and structure of the conical inferior appendages of the male genitalia.

Discussion

It is generally accepted that a great part of Southeast Asia consists of continental blocks that came from the supercontinent Gondwana, gradually moved northward, and docked with Southeast Asia during the Mesozoic. Gondwana had already broken off into two blocks about 130 million years ago: West Gondwana (Africa and South America) and east-Gondwana (India, Madagascar, Australia, Antarctica, and New Zealand) (McIntyre et al. 2017). The so-called West Burma Block is one of the continental blocks that split off from east-Gondwana at least 120–125 million years ago (Metcalfe 1996; Scotese 2014; Westerweel et al. 2019), gradually moved northward as an island in the Tethys Ocean over the course of

more than 20 million years (Heine et al. 2004; Seton et al. 2012), and is finally placed in the form of a broad band from south to north in Myanmar (Fig. 7). In northern Myanmar, the Hukawng Valley is located in the northern area of the elongated West Myanmar Block, with an area of about 5.5 square miles, surrounded by low mountains. In line with the hypothesis of Gondwanan origin, the West Burma Block and consequently the Hukawng valley are located as a Gondwanan island within the Laurasian region of Myanmar.

The Burmese amber is from the Hukawng Valley in the West Burma Block (Poinar 2018) and is dated to the mid-Cretaceous (Cenomanian) about 98.8 ± 0.6 Ma ago (Shi et al. 2012). The amber is rich in plant and animal inclusions. The predominant arthropods are currently recorded in 8 classes, 66 orders, 624 families, 1,491 genera with 2,349 species (Ross 2023). The numerous finds in Burmese amber raise the question of the origin of the organisms, whether they are from Gondwana and/or Laurasia. If the hypothesis of the Gondwanan origin of the Burmese amber and its paleobiota is correct, Gondwanan organisms and their descended lineages of the ca. 20 million years of oceanic island life are to be expected first. Only after that, Laurasian organisms could have joined.

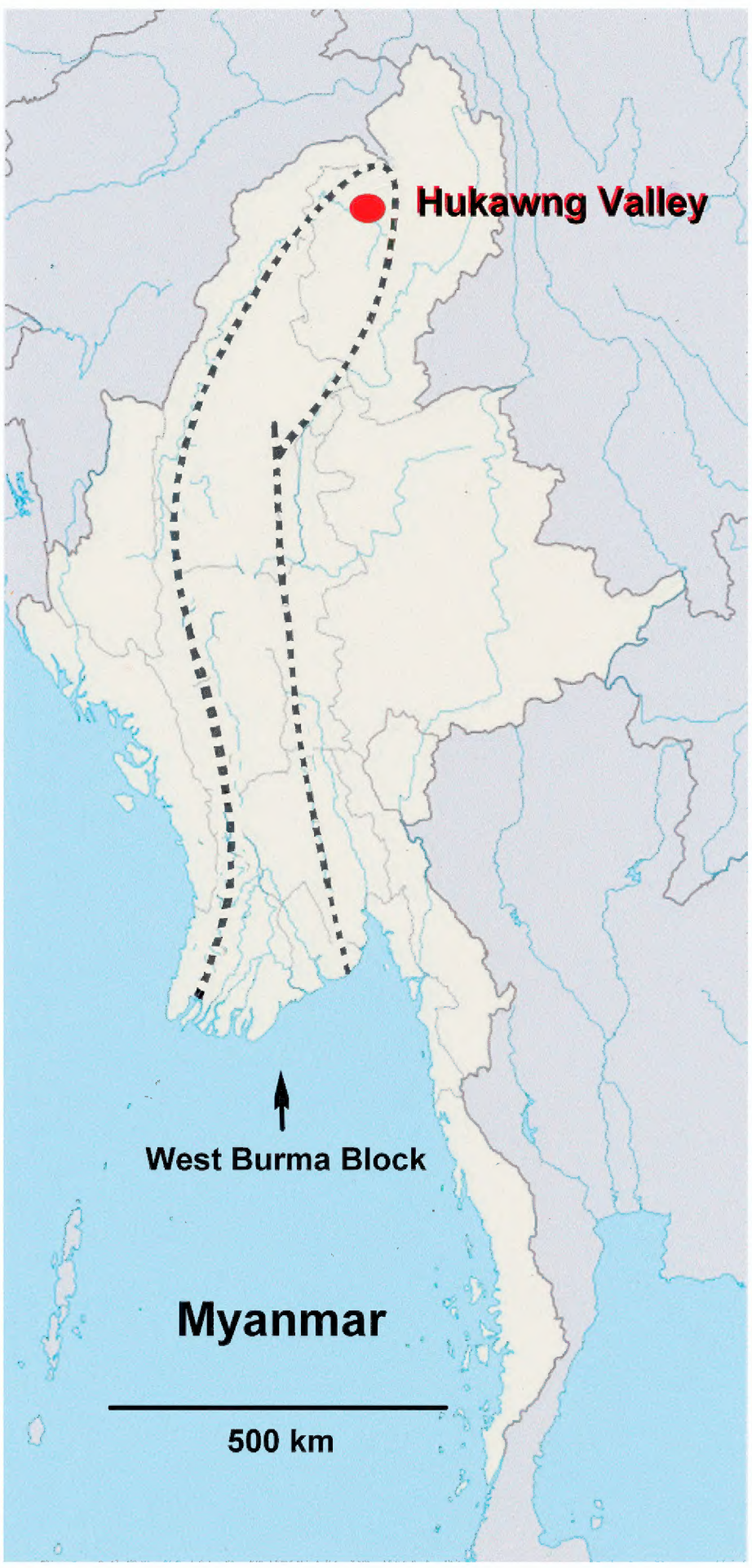

Figure 7. Drawing of Myanmar, with the West Burma Block in the center inside the dashed line and the Hukawng Valley in the north.

Fossil caddisflies embedded in Burmese amber have an age of about 100 million years (mid-Cretaceous) and are most likely derived from Trichoptera of Gondwana, assuming that the West-Burma-Block containing the Hukawng amber is from Gondwana. However, it cannot be excluded that caddisflies from Laurasia may appear in addition to caddisflies from Gondwana, even though the majority probably originated from Gondwana.

The current Trichoptera checklist (Table 1) includes 14 families, of which four Integripalpian families, Burmapsychidae, Cretapsychidae, Lepidochlamidae and Palleptoceridae, are extinct and only found in Burmese amber. Very probably these extinct families have Gondwanan origin. They belong to the infraorder Brevitentoria and are assigned to the superfamilies Sericostomatoidea (Burmapsychidae, Cretapsychidae) and Lepidostomatoidea (Lepidochlamidae, Palleptoceridae). Both superfamilies have their origin or at least basal stem forms in the southern hemisphere (Thomas et al. 2020). The Sericostomatoidea separated from the Leptoceroidea around 135 Ma of early Cretaceous (Malm et al. 2013), about the same time when Gondwana split into west- and east-Gondwana (McIntyre et al. 2017). After that the West Burma Block separated from the east-Gondwana. In line with the hypothesis of Gondwanan origin of the West Burma Block and the Burmese amber their extinct Trichoptera families may be descended from the Gondwanan and Neotropical infraorder Brevitentoria.

The Burmese amber continues to reveal more information about the evolutionary history of Trichoptera. For example, the family Xiphocentronidae is distributed in the Neotropic and Oriental regions. The Burmese amber is located in the Oriental region in northern Myanmar and preserves extinct species of the genus *Palerasnitsynus*, which establish the subfamily Palerasnitsyninae stat. nov. of Xiphocentronidae. However, *Palerasnitsynus* is not closely related to the Xiphocentronidae genera, which occur in the Oriental region. The extinct genus of middle Cretaceous may be descended from a Neotropical lineage of Xiphocentronidae, on the basis that the hypothesis of a Gondwanan origin of the Burmese amber is correct.

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